

## Mating Aggregation in the Japanese Treefrog, *Rhacophorus arboreus* (Anura: Rhacophoridae): a Test of Cooperation Hypothesis

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**ABSTRACT**—The hypothesis that the relationship among males in one female-multiple male aggregations in mating and oviposition of the foam-making rhacophorid frogs is cooperative was tested in the Japanese treefrog *Rhacophorus arboreus*. Joining males were not observed beating the foam with their hind limbs. The size of foam nest tended to increase with the body size of female, but was not correlated with the number of joining males. The duration of oviposition was correlated with the number of joining males but not with the body size of the paired female and male. These results were inconsistent with the hypothesis that the relationship among males in the one female-multiple male aggregations is cooperative.

### INTRODUCTION

Contrasting with conflicts among males at the scene of mating, cooperation among males during mating has been rarely reported, except cases where the high degree of relatedness among males is expected (e.g. [1]). However, in some foam-nesting rhacophorid treefrogs, the relationships among males in one female-multi male mating aggregations have been described as cooperative (e.g. [2] for *Chiromantis rufescens*; [3] for *Rhacophorus arboreus*). Following Coe [2], Wilson [4] considered a one female-three male aggregation of the African rhacophorid *Chiromantis rufescens* reported by Coe as a case of "cooperative breeding". In their review on the sperm competition in amphibians, however, Halliday and Verrell [5] pointed out that there is no evidence for Wilson's interpretation except the observation that all the males in the aggregation moved their hind limbs and contributed to the formation of the foam nest.

The behavioral sequences of mating of foam-nesting rhacophorid treefrogs in one female-multi male mating aggregations are: the pair in amplexus and some other males (hereafter referred to

joining males) arrive at the oviposition site (joining males sometimes arrive after the female begins oviposition). Only one male is in the amplexus position. The female secretes a fluid from which the foam nest is constructed and oviposits eggs into it. The female (and males in a few reports) beats the secretion and constructs the foam nest. After oviposition, the female and males leave the constructed foam nest.

In the present paper, we test two sub-hypotheses ("a larger nest hypothesis" and "less susceptibility of predation hypothesis", [2]) derived from the assumption that the male-male relationship in one female-multiple male mating aggregations is cooperative in the Japanese treefrog *R. arboreus*.

### MATERIALS AND METHODS

The observations were made from May to July, 1984, at the 'Hyoutan' pond (26 m×8 m) in Iwamuro, Niigata, Japan (altitude about 200 m). Frogs were captured by hand or with a handy net, and were individually marked with colored waist bands for later identification [6]. We measured the snout-vent length (body size, hereafter) and weight of each frog. Observations at night were made with a 6V battery head lamp which seemed not to disturb the behavior of frogs. We observed

the behavior of solitary females and pairs in amplexus and that of males approaching the observed females or pairs under observation. The length and width of newly deposited foam nest were measured (the method of [7]) with a ruler. The product of length and width was used for the size measurement of foam nest and called it 'size' of foam nest hereafter.

## RESULTS

During foam nest construction, we observed no males of beating the foam with their hind limbs (swimming-like behavior) apart from passive movements when the hind limbs of females touched those of males. In all the instances ( $n=14$ ), beating of the foam with hind limbs was done by females.

There is no significant correlation between the size of foam nest and the number of males in a mating aggregation ( $r=-0.194$ ,  $0.8>P>0.5$ ,  $n=11$ ) (Fig. 1).

The size of foam nest is not significantly correlated with the body size of the female ( $r=0.451$ ,  $0.05<P<0.1$ ,  $n=16$ , Fig. 2), although there is a trend suggesting the female body size is one of factors governing the size of the foam nest. There is no significant correlation between the size of foam nest and the body size of the male in amplexus ( $r=0.042$ ,  $P>0.8$ ,  $n=9$ , Fig. 3).

There is no correlation between the number of males in a mating aggregation and the body size of the male in amplexus ( $r=-0.039$ ,  $P>0.8$ ,  $n=10$ ) nor the size of the female ( $r=0.263$ ,  $0.5>P>0.4$ ,

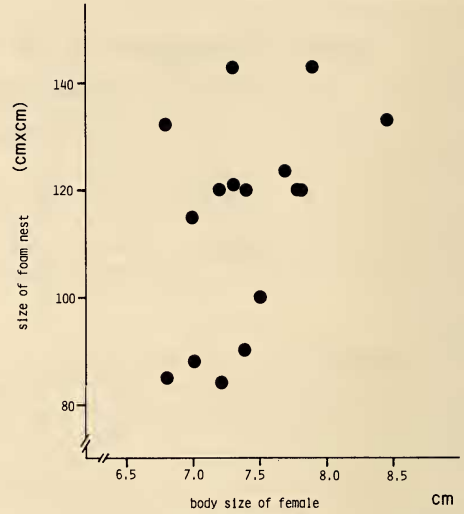


FIG. 2. The relationship between the size of foam nest and the body size (snout-vent length) of the female.

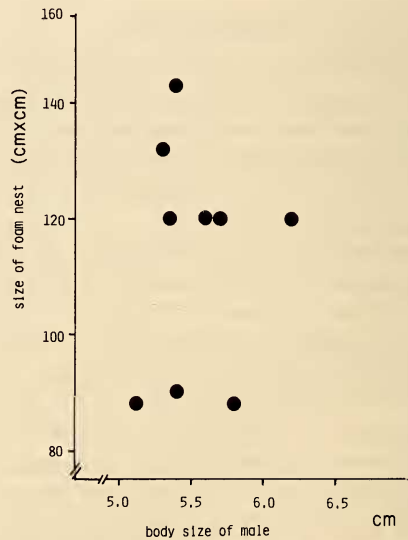


FIG. 3. The relationship between the size of foam nest and the body size (snout-vent length) of the male in amplexus.

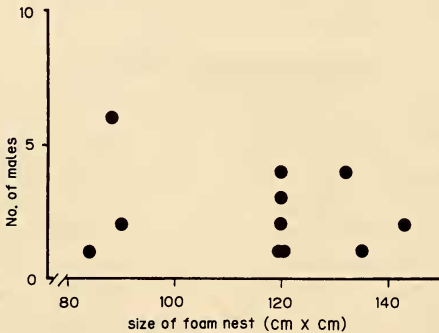


FIG. 1. The relationship between the size of foam nest and the number of males in mating aggregation.

$n=11$ ).

Figures 4 and 5 show the relationships between the duration of oviposition (from the beginning of construction of foam nest, i.e. the swimming movement of hind limbs of female, to the leaving of the female) and the number of males in mating

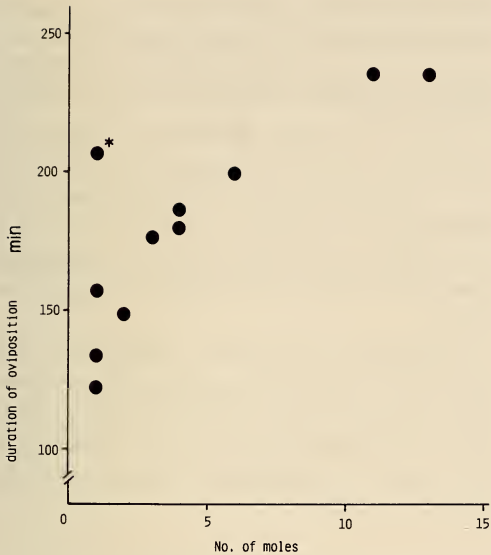


FIG. 4. The relationship between the duration of oviposition (from the beginning of foam nest construction to the departure of the female) and the number of males.

asterisk: the amplexus posture of male (grip of his fore limbs) was incomplete.

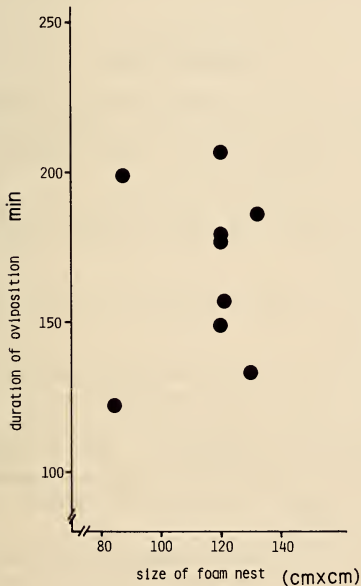


FIG. 5. The relationship between the duration of oviposition (from the beginning of foam nest construction to the leaving of the female) and the size of foam nest.

aggregation and the size of foam nest, respectively. There is a significantly positive correlation between the duration of oviposition and the number of males ( $r=0.820$ ,  $P<0.05$ ,  $n=11$ ) (Fig. 4). However, the correlation between the duration of oviposition and the size of foam nest is not significant (Fig. 5,  $r=0.077$ ,  $P>0.8$ ,  $n=9$ ). The correlation between the duration of oviposition and the body size of female is also not significant ( $r=0.134$ ,  $0.8>P>0.5$ ,  $n=10$ ).

## DISCUSSION

First, we test the following two sub-hypotheses derived from the main hypothesis that the male-male relationship in mating aggregations is cooperative. They are "a larger nest hypothesis" [2]: the advantage of using more than one male is that a larger nest can be constructed (and thus a larger number of offspring can be reared), and "less susceptibility of predation hypothesis" [2]: the advantage of using more than one male is that the assistance by a larger number of males render a female less susceptible to predation because the oviposition activity leaves the female exhausted.

The first sub-hypothesis predicts the positive correlation between the size of foam nest and the number of males. However, this is inconsistent with the result of Figures 1 which shows weakly negative (not significant) correlation between them. The results of Figures 1 and 2 suggest that the factor responsible for the size of foam nest is not the number of males but the body size of female.

The second sub-hypothesis is not directly tested because we did not measure the degree of exhaustion of females after oviposition. We use the duration of oviposition as a substitute. Furthermore, the duration of oviposition seems to be a reasonable index of susceptibility of predation during oviposition. *R. arboreus* was preyed by predators including snakes during oviposition (e.g. Kinefuchi, personal communication). The results of Figures 4 and 5 show that the duration of oviposition is strongly positively correlated with the number of males and is not correlated with the size of foam nest.

Therefore, both sub-hypotheses of the coopera-

tion hypothesis are not consistent with the results of the present study.

The cooperation hypothesis is not consistent with the observation by Saitou and Kumaki (unpublished) that the hatchability of eggs in cases of one female–multi male mating aggregations is similar to that in oviposition by a single pair in amplexus (96.4% and 98.6%, respectively). Furthermore, Kato [8] reported that all the males in mating aggregation secrete sperm with both direct and microscopic observations.

We propose alternative hypothesis, “sperm competition hypothesis”, for explaining the significance of one female–multi male mating aggregation in foam-making rhacophorids based on the results of the present study. This suggests that one female–multi male mating aggregations are formed as a consequence of selfish activities of joining males, i.e. releasing sperm into the foam and fertilizing eggs by his own sperm. Because interruption of the oviposition is costly for both female and male of the pair, and because the male in the amplexus can not use his fore limbs [5], both female and male of the pair can not effectively counteract other males which approach the pair to release sperm into the foam. In this hypothesis, the joining of males is regarded as detrimental for both the male and female in amplexus. For the female, the joining males increase the duration of oviposition and hence increase the susceptibility of predation. For the male, they decrease the number of eggs fertilized by his sperm and increase his susceptibility of predation. The “sperm competition” hypothesis is consistent with the results of the present study.

Males joining the mating aggregation do not increase the size of the foam nest (Fig. 1). The size of foam nest is not correlated with the body size of male in amplexus nor the number of males (Fig. 3), but there is a trend between the foam nest and the body size of female (Fig. 2). The activities of males are not responsible for the size of foam nest. It suggests that the body size of female determines the size of the foam nest. The joining of males is costly in terms of the duration of oviposition (Figs. 4 and 5). The activities of joining males in mating aggregation are thus considered to be obstructing the constructing behavior of female rather than

assisting it. In the present study, this is a natural conclusion because we did not observe the swimming-like behavior of hind limbs of males in mating aggregations. This does not mean, however, that the male–male relationship is cooperative in species in which the swimming-like behavior of males is observed (e.g. [2, 7]). In such species, the swimming-like behavior of males can be interpreted either as cooperative behavior or selfish one to increase the chance of fertilization of eggs by his sperm.

In conclusion, the selective significance of one female–multi female mating aggregation in foam-making rhacophorids is better explained by selfishness of males than by cooperation of males, as in the context of reproductive behavior of other anurans (e.g. [9]).

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